TERRITORIAL AGGRESSION IN WINTERING WARBLERS AT BAHAMA AGAVE BLOSSOMS

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The massive yellow flower heads of the century plant (*Agave Braceana*) provide rich localized sources of nectar and insects on the northern Bahama Islands during the late winter of each year. Scattered every few hundred feet through parts of the extensive open pine forests, these showy plants, 4 to 7 meters tall, attract large numbers of a wide variety of permanent resident and migrant birds during their brief period of flowering. Bananaquits (*Coereba flaveola*) and Cuban Emerald Hummingbirds (*Chlorostilbon ricordii*) are prominent among the resident species, with smaller numbers of Olive-capped Warblers (*Dendroica pityophila*), native Yellow-throated Warblers (*Dendroica dominica flavescens*) and Red-legged thrushes (*Mimocichla plumbea*) making frequent visits. Among the wintering migrants from North America the Palm Warbler (*Dendroica palmarum*) is most numerous at the blossoms, while Cape May Warblers (*D. tigrina*), Myrtle Warblers (*D. coronata*), Eastern Yellow-throated Warblers (*D. d. dominica*), Prairie Warblers (*D. discolor*), Yellowthroats (*Geothlypis trichas*) and Catbirds (*Dumetella carolinensis*) make frequent appearances.

The scene at each plant is characterized by frenzied chasing through much of each day. Birds alight and are replaced at frequent intervals, and only a few individuals besides the large thrushes and Catbirds and the stubbornly defiant Bananaquits manage to remain for more than 10 to 15 seconds at a time. Although no birds were tagged for individual identification in this study, close watching revealed that a single large plant often served as the continuing focus for aggressive activities of a particular bird for an hour or more and, possibly over several consecutive days.

On the morning of 25 January 1971, I followed all activity on one large agave near Fortune Bay, Grand Bahama Island for 55 consecutive minutes. During this period the plant was persistently dominated by a male Cape May Warbler. In a 25-minute test period the bird spent about 20 percent of the time chasing intruders, about 70 percent sitting on look-out perches within 12 meters of the agave top, and only about 10 percent actually feeding. Conforming to the usual pattern of local wintering warblers the bird did not sing. During these 25 minutes the plant was approached by five Palm Warblers, two Northern Yellowthroats, six Cuban Emeralds, and seven Bananaquits. All intruders of the first three species were quickly and vigorously attacked, some of them when they were still 6 to 8 meters away from the agave. The warblers invariably retreated; a few hummingbirds succeeded

in returning and feeding briefly on the back side of a blossom, apparently hidden from view. The Bananaquits, by contrast, persisted. Although smaller than the warbler they flew in directly and fed freely making little or no response to the warbler who approached hesitantly in three instances to perch about a meter away and then fly back to a nearby lookout perch. In no case was the resident warbler seen to feed while the Bananaquits were present. In no case were the Bananaquits seen to attack any visitors to the plant.

On 28 January I watched the activity at five agaves in the same area for uninterrupted periods of 10 to 20 minutes each. Palm Warblers dominated at four of these plants; no single bird dominated in the fighting at the fifth plant, the one held by the Cape May Warbler three days before. At each of the dominated plants all intruding warblers and hummingbirds were vigorously repelled before reaching the blossoms. The behavior was similar to that of the Cape May Warbler, and again, no singing occurred. Repelled species included other Palm Warblers, Cape May Warblers, Yellow-throated Warblers, migrant Yellowthroats, Olive-capped Warblers and Cuban Emeralds. As with the Cape May Warbler on the 25th, Bananaquits were grudgingly tolerated in all cases. Two Catbirds and one Red-legged Thrush which visited were not challenged and remained feeding for several minutes. Activity on the non-dominated agave was difficult to interpret, but irregular chasing by warblers of at least three species, stubborn unconcern by Bananaquits and timid persistence by hummingbirds was observed.

The persistence of the established Cape May Warbler and the four Palm Warblers in repelling birds that approached their plants indicates that more was involved than simple aggressive responses to imposed crowding. In each case a single individual vigorously assumed and retained dominance over conspecifics and a variety of other challengers for appreciable periods of time. Such energy-expensive behavior calls for consideration of the associated circumstances and the potential advantages.

Localized aggression by temporarily established individuals is a familiar phenomenon with various birds at artificial feeding stations in temperate regions where food is locally concentrated in an otherwise impoverished winter environment. Hummingbirds of various species show similar behavior in flower gardens or at seasonally flowering trees where, again, a special food supply is concentrated within a small area (Pitelka, 1942; Armitage, 1955; Stiles and Wolf, 1970). Birds that utilize dispersed food resources such as the insectivorous warblers have rarely been observed in such behavior in their winter quarters, and in the two cases known to me a regional shortage of natural foods was suspected. In one case (Woolfenden, 1962), a Myrtle Warbler established itself for 14 days on an area of green lawn in Gainesville, Florida, during a particularly cold spell, driving off all intruding war-

blers and kinglets. In the other (Kale, 1967), a migrant Cape May Warbler on Dry Tortugas repeatedly attacked and repelled warblers of several species for three consecutive days whenever they approached a particular agave blossom.

Agave blossoms clearly provide an extremely rich as well as spatially concentrated source of nectar and insects. A corresponding concentration of nectar and insect feeding birds in the Grand Bahama situation is, therefore, not surprising. Intense aggressive activity, on the other hand, would be uneconomical unless the food supply in the surrounding area was so poor as to require a comparable or greater expenditure of energy in search and pursuit of prey. In the present instance the energy cost of aggressive activity appears to have been very high (roughly 90 percent of the bird's time in the one instance where it was evaluated), while the availability of food in the surrounding areas was apparently great as judged by the maintenance of high insectivore densities through the winter and spring and by direct evidence of continuing high arthropod populations and nectar sources before and after the agave blossoming season (unpublished data).

Mild dominance behavior and subtle supplanting of intruders by locally established individuals during the non-breeding season has been observed in a variety of birds (Kluijver, 1951; Kluyver and Tinbergen, 1953; Gibb, 1960; Brown, 1963) and appears to function in the selective survival of established local residents in situations of food scarcity. Vigorous and persistent repulsion of intruders in situations of regional food abundance is quite a different matter, however, and is rarely encountered except in nesting situations.

We have, of course, very little information on the relative food values of nectar *vs* insects, the energy costs of aggressive chasing *vs* foliage gleaning, or the particular conditions applying at the site of the observed episodes on Grand Bahama. I am inclined, however, to interpret the behavior described in this report as extravagant and maladaptive, and to attribute its persistence in the face of natural selection to the graded nature of aggressivity as related to stimulus intensity, and to the unusual and transitory nature of the situation that elicited it. Territorial aggression, beneficial at low intensities, promptly becomes detrimental when it rises in intensity to the point where energy cost exceeds derived value. Special intensity regulating mechanisms could conceivably evolve to alter the stimulus-response curve at the appropriate point, but where the critical situation that produces the detrimental response level occurs only rarely and briefly, the fine adjustment of the genotype needed to effect the adaptation may be impractical.

In conclusion, I propose that the energy-expensive overt aggression displayed by these birds is a transitory and maladaptive over-extension of a normally mild territorial dominance precipitated by the sudden appearance of a concentrated swarm of invaders on their feeding territories.

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